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Two Social Halictine Bees from Southern Mexico with a Note on Two Bee Hunting Philanthine Wasps (Hymenoptera: Halictidae and Sphecidae)

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On the 25th of January 1985 a large mixed aggregation of *Halictus* (*Seladonia*) *hesperus* Smith and *Lasioglossum* (*Dialictus*) *exiguum* (Smith) was discovered 1 kilometer to the east of Ocosingo, Chiapas, Mexico. Bees of both species were abundant along the length of a bank at the side of a dirt road. The vertical face of the bank was bare but the top was covered in vegetation that was kept short by the grazing activities of a herd of bulls. The bank varied in height from 30 to 125 cm and the bees appeared to be congregated mainly where the bank was at least half a meter in height. The lower portion of the bank had been cut back by machinery earlier that morning and many bees were searching for their destroyed nests. Other nests with entrances near the top of the bank remained intact. Samples of flying bees were collected and nests excavated on the 25th and 26th of January. Nests were excavated by pushing a grass stem down the burrow entrance and digging from the side of the bank. The bees were killed and preserved in 70% alcohol and measured, aged and dissected using standard techniques (Abrams and Eickwort, 1980).

The nesting substrate was complex, being composed of a mixed series of deposits from the nearby river overlain by a loam layer some 10 to 15 centimeters deep. The substrate beneath was largely composed of compacted sand interspersed with bands of clay and limestone. Both species seemed to nest only on the vertical exposed surface of the bank, avoiding the flat area above where some *Halictus ligatus* nests were found. *H. hesperus* nests had been initiated in the dark topsoil layer but *L. exiguum* nest entrances were found both in the dark soil and the sandy vertical faces.

A small aggregation of *Philanthus gibbosus* Fabricius nests was located in the vertical sandy part of the bank in an area with many nests of both halictine species. Three nests were excavated and two females returning with prey were captured. *Trachypus gracilis* Cameron and *T. mexicanus* Saussure nested in loose aggregations in the area, no nests of these species were excavated but two females of the former were caught returning with prey.

Ocosingo is situated in a valley (17°10′N, 92°26′W) at an altitude of about 800 meters and is bordered to the north and south by mountains that exceed 2000 meters in height. The dry season in this part of Mexico begins in November and ends in April.

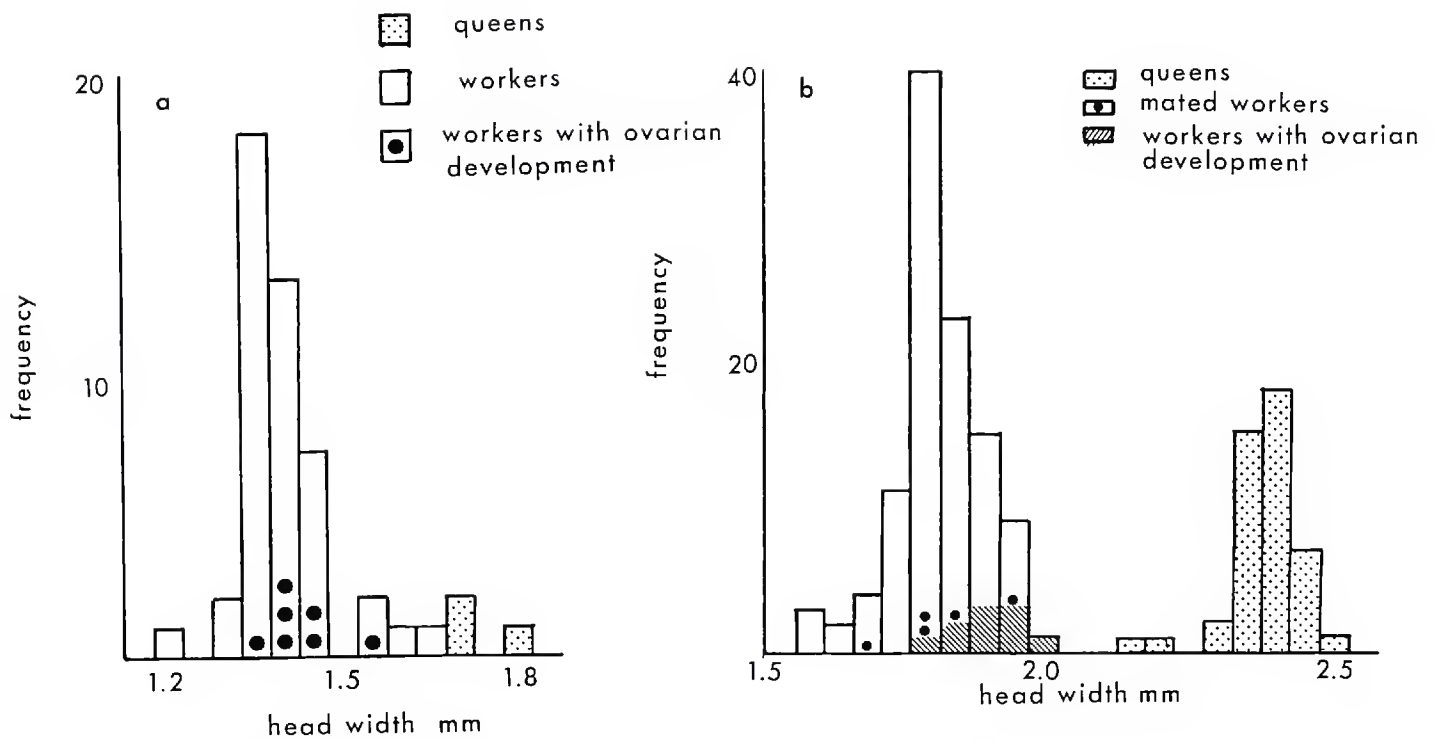

Figure 1. Histograms showing size variation and reproductive status of a) *L. exiguum* and b) *H. hesperus* females.

Results

Thirty-four workers and three queens of *L. exiguum* were caught flying around the nest site and an additional 11 workers came from an incompletely excavated nest.

The queens were obviously larger than the workers and were the only bees that had mated (Fig. 1a). Queens averaged 19.5% larger than the workers based upon head width and 19.2% larger in wing length (mean and standard deviation of head width—queens $\bar{x} = 1.73$, SD = 0.047; workers $\bar{x} = 1.39$, SD = 0.52; wing lengths—queens $\bar{x} = 4.35$, SD = 0.084; workers $\bar{x} = 3.51$, SD = 0.14).

Seven (15.2%) of the workers had enlarged ovaries and 5 (10.9%) contained an oocyte that was at least half developed. Each of the three queens contained a minimum of two oocytes that were more than half developed.

Two nests were incompletely excavated. One contained 11 workers one of which had developed ovaries. The nest burrow was horizontal from the vertical sand bank for about 20 centimeters and then sloped down at an angle of 30 degrees from the horizontal for another 25 cm before it was lost. One branch left the main burrow 25 cm in from the entrance and continued parallel to it for approximately 10 cm. The nest entrance was about 2 mm across and guarded, the burrows were 3 mm in diameter. No cells were located in this nest. The other nest had been opened by the cutting back of the bank, no adult bees were located, but four worker pupae and a fully grown larva were found. The cells were about 9 mm in length and 3 mm in height with a narrow neck that was from 2 to 3 mm in length and were lined with a waxy like material as is usual in halictines.

Ninety-three workers and 38 queens of *H. hesperus* were caught flying around the nest site and a further 15 workers and 7 queens excavated from nests. As with *L. exiguum,* the queens were much larger than the workers (Fig. 1b) averaging 23.4% larger based upon head width and 19.5% larger in wing length (mean and standard deviation in head width, queens—$\bar{x} = 2.38$, SD = 0.07; workers $\bar{x} =$

1.82, SD = 0.08; wing length, queens—$\bar{x}$ = 5.83, SD = 0.09, workers $\bar{x}$ = 4.79, SD = 0.16).

Six (5.5%) of the workers had mated and 10 (9.3%) had enlarged ovaries, 5 of them with an oocyte at least half developed. Mated workers were no larger than unmated ones (mean head width of mated workers 1.82) but those with ovarian development were significantly larger (mean head width of workers with developed ovaries $\bar{x}$ = 1.89, SD = 0.06; for the rest $\bar{x}$ = 1.81, SD = 0.07, t = 3.27, $P <$ 0.01).

Most of the workers had extremely worn mandibles, often worn down to the inner tooth or beyond even if the wings showed no signs of wear.

Six nests were fully excavated, three contained only the founding gyne, the remainder are illustrated in Figure 2. The entrances of all three illustrated nests were constricted to a diameter of 2 mm (narrower than the head widths of the queens) burrow diameters being about 4 mm. The cells were lined with a waxy material as is usual for halictines and the top parts of the burrows were lined with paler soil from deeper in the nest. No chalky film was observed lining the upper part of the burrows. The nests with solitary gynes did not have constricted entrances and the upper parts of the burrow were not lined with material from lower down. As can be seen from Figure 2 the most recently excavated cells were not necessarily the deepest and in nest 1 were well spread amongst the older ones. Nest contents are shown in Figure 2; all of the pupae were female and clearly of worker size.

Two queenright nests contained 8 and 5 workers, the third nest contained two workers and a dead queen. In the last case neither of the workers were mated or had ovarian development but both had mandibular wear.

Some *H. hesperus* gynes were still in the early stages of colony founding. This is indicated by the three excavated nests that contained only the foundress and the presence of gyne-sized bees with little ovarian development and low indices of wear amongst the bees caught flying around the nest site.

A bombyliid fly *Bombylius* sp. was observed flying around areas inhabited by *H. hesperus.* The association between the fly and its possible host was not confirmed but flies of this genus frequently attack halictine bees. A deutonymph of *Anoetus* sp. (Acari: Histiostomatidae) was found on a fully grown larva of *H. hesperus,* these mites are common associates of halictines (Eickwort, 1979).

Two females of each of *Philanthus gibbosus* and *Trachypus gracilis* were caught returning to their nests with prey. Each of the wasps was carrying a worker of *H. hesperus.* A small aggregation of *Philanthus gibbosus* nests was found in the vertical, sandy part of the bank, in close proximity to nests of the two halictine species. The exact positions of *Trachypus gracilis* nests was not determined but judging by the behavior of several females they made their nest entrances in the darker surface soil in the portion that was overhung by grass roots. *T. mexicanus* females also nested in the vertical side of the bank.

Philanthus gibbosus females were observed to close their nest entrances while foraging and when in the burrows for any great length of time. The nest entrances were roughly semicircular with a lower diameter of 6 mm and a height of 4 mm. The burrows were more or less horizontal but curved to the left and right. No accessory burrows were observed. Two cells were discovered in one nest and one in each of the other two. Cell contents were as follows:

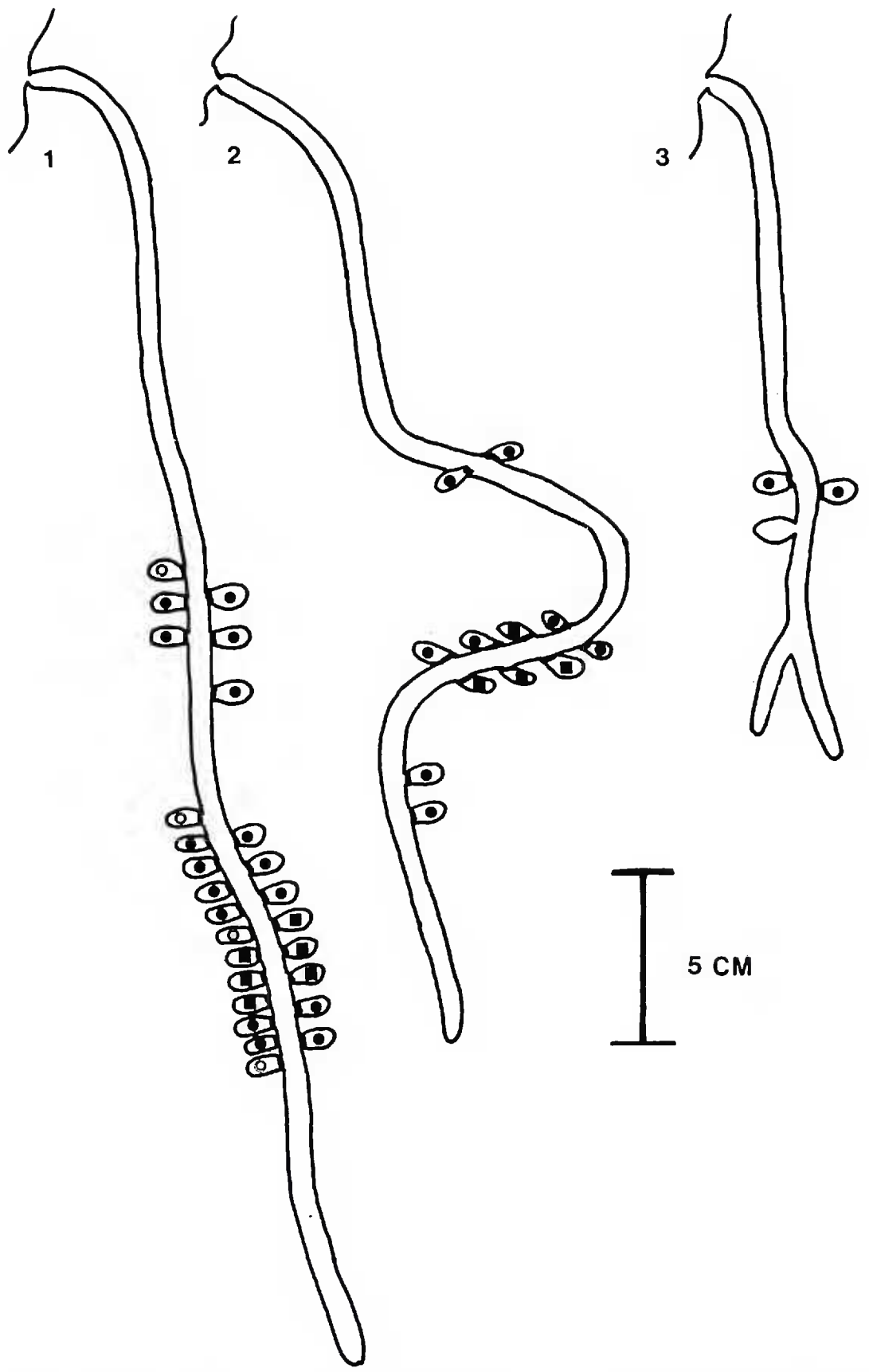

Figure 2. Three nests of *H. hesperus*. The open circles represent pollen balls, with or without eggs; closed circles are larvae and squares represent prepupae and pupae. The open cell in nest 3 had been newly excavated and the dead gyne in this nest had been pushed to the bottom of the right hand branch of the burrow. Filled in cells are not shown in the diagrams because their number and positions are not known with any accuracy.

Nest 1. Cell 1.—5 *H. hesperus* queens, 1 *L. exiguum* queen. Cell 2.—4 *H. hesperus* queens.
Nest 2. Cell 1.—5 *H. hesperus* workers, 1 dead *Philanthus* female.
Nest 3. Cell 1.—10 *H. hesperus* workers.

Two *P. gibbosus* males were captured while escaping from one burrow when a long piece of grass was pushed into the entrance.

Discussion

Halictus hesperus has been the subject of two previous reports: Wille and Michener (1971) studied the species briefly in Costa Rica and Brooks and Roubik (1983) made their observations from the middle to near the end of the colony cycle in Panama. The data presented here represent an earlier stage of the colony cycle than in the Panama study. Some of the differences between the studies may be attributable to this. For example, the size difference between queens and workers is greater in the bees from Southern Mexico than Panama (the percentage size differences being 23.4 and 15.2 respectively based upon head width). An increase in worker size during the colony cycle is a well known phenomenon in social halictine species with more than one worker brood (Breed, 1975). Thus a larger size difference between queens and workers is to be expected earlier in the colony cycle. Similarly the lesser degree of ovarian development in workers from Mexico (9% showing any ovarial development) compared to the populations from Panama and Costa Rica (25 and 30.1% respectively) may be attributed to an earlier stage of colony development. Thus the queen may more easily dominate the fewer number of smaller workers particularly when she is younger.

Both previous studies reported the existence of a chalky lining to the top of the burrow. This product of the Dufours gland (Brooks and Cane, 1984) was not observed in the nests in Mexico. Brooks and Cane (1984) suggest that the function of this secretion is to cement together the soil particles at the nest entrance. The lack of this lining in the Mexican nests supports this hypothesis because with the nest entrances situated on a near vertical slope loose soil particles did not collect around the entrance. In contrast, the nests in Panama and Costa Rica were on level ground.

The high levels of worker mandibular wear found in *H. hesperus* at Ocosingo are quite remarkable, almost half of the bees having mandibles worn down to the level of the inner tooth. This may be because the workers enlarge the nests before commencing foraging activities, the very hard, compacted substrate causing a large amount of mandibular wear. A similarly high degree of worker mandibular wear was observed by Wille and Michener (1971).

This is the first description of the biology of *L. exiguum* a species known only from southern Mexico. However, it is very closely related to *L. umbripenne* which has been found in Guatemala and Costa Rica (Eickwort, 1970). These two taxa may be sibling species, or differentiated only at the subspecific level (Eickwort, pers. comm.).

L. umbripenne has been studied in two localities in Costa Rica by Wille and Orozco (1970) in the distinctly seasonal habitat of Damitas and Eickwort and Eickwort (1971) in the more homogeneous climate of Turrialba. Eickwort determined that the bees at the two localities were conspecific (Eickwort 1970). The scanty data available on the social organization of *L. exiguum* indicate that it is more similar to *L. umbripenne* in details of its biology than any other member of the subgenus *Dialictus* that has been studied so far. Thus, both species exhibit a large degree of morphological caste differentiation (size differences, based upon wing lengths being 19.2% for *L. exiguum,* 16.9% for the Damitas population of *L. umbripenne* and 9.1% at the Turrialba locality). There is a similar degree of queen control over worker reproductivity in the two species. With respect to

ovarian development 15.2% of the *L. exiguum* workers had developed ovaries whereas the corresponding figures for *L. umbripenne* are 34 and 25% at Damitas and Turrialba respectively. None of the *L. exiguum* workers were mated whereas in the larger samples of *L. umbripenne* 2.5% were mated at Damitas and 6.1% at Turrialba.

Unfortunately, insufficient data from nest excavations are available to investigate other variables that pertain to the social organization of *L. exiguum.* Particularly important would be data concerning the frequency of polygynous nests. However, judging from the, admittedly small, samples of flying bees it seems likely that small gynes may not occur in this population making it more similar to the Damitas population of *L. umbripenne* than the Turrialba one. The caste differentiation data are in agreement with this comparison. The differences between the data for the two species may, in part, be due to the small sample size for the Mexican species. However, these four variables (queen-worker size dimorphism, queen control over worker ovarian development and mating and the degree of polygyny) are important in halictine social evolution (Breed, 1976; Packer and Knerer, 1985) and the fact that all indicate a higher social level for *L. exiguum* may be significant. Additionally, the data indicate that the Mexican species is more similar to the Damitas population of *L. umbripenne* than the Turrialba one. This may not be surprising considering the more marked wet and dry seasons at the former two localities compared to Turrialba.

The data on *H. hesperus* and *L. exiguum* are consistent with the notion that these species begin their colony cycles in the dry season. The absence of any adult males of either species around the nest site or on flowers in the surrounding area or of male pupae in the nests of *H. hesperus* indicate that only the earlier stages of the colony cycle are present at this locality in January.

The data on *H. hesperus* indicate that although some nests contained developing second brood workers others consisted of a solitary gyne which had not yet begun provisioning. The comparatively low index of mandibular wear and the poorly developed ovaries of some of these gynes strongly suggest that they were not merely foundresses that had lost their nests and brood during the bank widening process. This indicates an unusual lack of synchrony in nest initiation in this species. A small sample of *H. hesperus* collected from the flowers of *Bidens pilosa* along an undisturbed roadside at a lower elevation at nearby Palenque also contained worn workers and queens. Such lack of synchrony in nest initiation has been observed in *L. umbripenne* (Wille and Orozco, 1971) and also in *Lasioglossum* (*Evylaeus*) *malachurum* (Knerer, 1973). In the latter instance nest initiation was bimodal with the second peak representing bees that had been trying to usurp the nests of others but initiated their own when the end of the first brood provisioning phase had been reached by the rest of the population. It is considered unlikely that *H. hesperus* gynes exhibit a similar dual strategy. Perhaps the transition from wet to dry season is not as easy to predict as the end of a cold winter which serves as a cue for nest initiation for temperate social halictines.

Trachypus gracilis, like *T. mexicanus* studied by Evans (1964) would seem to concentrate upon *H. hesperus* as prey. Evans found that 7 of the 9 bees caught by one *T. mexicanus* female belonged to this prey species, one other was of the halictid genus *Augochlora* and the last was an anthophorid bee *Exomalopsis.*

The behavior observed in *P. gibbosus* is no different from that which has been

previously described for this sphecid, with the exception of the prey species recorded here. Males of *P. gibbosus* are known to rest within the nest (Evans, 1973) and nest closure during hunting and while the female is inside the nest has also been reported (Evans and Lin, 1959). Burrow sharing has been recorded in several *Philanthus* species including *P. gibbosus* (Evans, 1973). This phenomenon was not observed at Ocosingo, perhaps because of the limited duration of the study.

P. gibbosus is known to concentrate upon halictine bees as prey (Evans and Lin, 1959; Barrows and Snyder, 1973; Alcock, 1974). It is interesting to note that *H. hesperus* may be the major prey species of *P. gibbosus, T. gracilis* and *T. mexicanus* at this locality, at least during the dry season. A high degree of overlap in prey speices has been observed for sympatric *Philanthus* on several occasions (Alcock, 1974 and references therein).

Summary

A nesting aggregation of *Lasioglossum* (*Dialictus*) *exiguum* and *Halictus hesperus* was discovered in the state of Chiapas, Mexico in January 1985. Both of these species are primitively eusocial with well developed morphological and physiological caste differentiation. *H. hesperus* has been studied in Costa Rica and Panama and details of the biologies of the different populations are compared. The social organisation of *L. exiguum* is compared with that of its close relative *L. umbripenne. Philanthus gibbosus* is recorded as a predator upon both halictine species and *Trachypus gracilis* preyed upon *H. hesperus.*

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